**Maunsell, John**
**1 October 1989 – 30 September 1992**

**N00014-90-J-1070**
**Final Technical Report**

*Overview:* The work in this project was directed at trying to understand the brain mechanisms that subserve higher visual functions. The approach used involved examining the activity of neurons in the brains of nonhuman primates while they are performing visual tasks that they have been trained to do. One of our primary interests is how populations of neurons create representations that support short term visual memories. To examine this question, we trained monkeys to perform matching tasks in which they are shown visual stimuli that they must remember for short periods. We have found that many neurons in visual cerebral cortex are selectively activated during periods when the animal is keeping a particular stimulus in mind. The activity of these neurons is likely to provide the basis for short term memories, and understanding the origin of this activity and its interactions with sensory signals will be an important step in understanding how the brain implements higher functions such as visual search.

*General Background:* Our earlier work showed that memory-related signals can be found even at relatively early stages of processing in visual cortex. The visual cortex in all primates, including man, is organized in a hierarchical fashion. Signals coming from the retinas in the eyes arrive at the primary visual cortex (striate cortex, or V1), which performs an initial analysis and then relays the information to other areas in visual cortex. These other areas perform further analysis and relay the results to still higher areas. The process is repeated many times, culminating in representations in the highest visual areas in the parietal and temporal lobes. In the rhesus monkey there are known to be at least 30 discrete areas in visual cortex, each representing a different type of information about the visual world.

Changes in neuronal activity related to memory, attention or motivation have been described by many laboratories in the highest levels of visual cortex, but whether they influence information processing in earlier stages had not been extensively examined. For this reason, we examined memory related activity in area V4, which is at an intermediate level of cortical processing, only two steps removed from the primary visual cortex. We trained rhesus monkeys to perform a task in which they had to remember the orientation of a briefly presented grating pattern, and we compared the activity of individual neurons in V4 while the animals remembered different orientations. We found that as many as half of the neurons in this area had different levels of activity depending on what the animal was remembering, with each neuron most active while the animal remembered a particular orientation. Collectively, these neurons provided an unambiguous signal about the orientation that the animal was remembering. It is likely that they contribute in an important way to the ability to remember different orientations.

Memory related signals in visual cortex provide a particularly valuable avenue for exploring the neural mechanisms of a higher brain function. Memory related neuronal activity can be examined during periods when no stimulus is present, and when no motor acts are being performed. This eliminates potential confounding factors and greatly simplifies interpretation of results.

*Progress:* During the funding period been working to better characterize the distribution of these signals in cerebral cortex, with the long term goal of understanding which brain structures they depend on and how they interact with sensory information in generating behaviors. We have focused the question of how memory related signals are distributed between the two streams of processing that exist in visual cortex. As information is transmitted to higher levels of cortical processing, it is divided into two streams of processing that subserve different visual functions. Each stream is made up of many cortical areas. One leads to parietal cortex, and is important for visual assessment of spatial relationships and movements. The other leads to the temporal lobe

and is important for recognition of pattern and shape. These streams have also been called the "motion pathway" and the "color and form pathway."

Area V4, in which we found activity related to short term memories, lies in the temporal (color/form) pathway. We wanted to see if similar memory related activity could be found in the parietal pathway, which subserves spatial and motion analysis. To do this we recorded from neurons in the middle temporal visual area (MT), which is an important element in the parietal pathway. We selected MT because it lies at the same hierarchical level of processing as V4, and because the stimulus preferences of its neurons have been extensively characterized. Neurons in MT are very sensitive to the direction of stimulus motion. They respond strongly when a stimulus moves through their receptive field in the preferred direction, and not at all if the same stimulus moves in the opposite direction. Because MT neurons are sensitive to direction, we used a matching task in which the animal was presented with patches of randomly-spaced dots, which moved coherently across the screen. The animals had to remember the direction of a briefly presented random-dot pattern, and we examined the activity of neurons in MT while the animals were remembering different directions.

We found few memory related effects in MT. We therefore went on to examined later stages of processing in the parietal pathway: the medial superior temporal area (MST), which receives output from MT; and area 7a, which is one of the highest levels of processing in the parietal pathway. Although these areas contained neurons with some memory-related activity, the effects were fewer and weaker than those we had seen in V4 during orientation matching.

This absence of pronounced effects in the parietal pathway led us to examine responses in V4 using the direction matching task. Although many neurons in V4 have a weak direction preference, very few are strongly direction selective, and we therefore did not expect to find many V4 neurons with memory related effects during direction matching. To our surprise, many V4 neurons showed memory related changes in activity when the animal was remembering different directions of motion. The effects were about as prevalent as those seen during the orientation matching task. Even neurons that responded equally well to any direction of stimulus motion were sometimes much more or less active while the animal was remembered particular directions of motion. These results were reported in a recent article in the Journal of Neuroscience, which is included in the appendix.

These results suggest that area V4, and presumably other areas in the temporal pathway, are important in tasks that involve short term memory, regardless of what visual stimulus is being remembered. Although the parietal pathway is generally associated with motion processing, it now appears that it is not involved in all classes of motion analysis. We believe that the parietal pathway may be specifically adapted to serving the needs of visual guidance and navigation, and may not be involved in evaluating other types of movements in the environment.

*Future Directions:* Determining the functional specialization in the nervous system will be important for understanding how the nervous system efficiently allocates resources for executing complex behaviors. Although our research is no longer supported by the Office of Naval Research, we have be able to continue some research on these questions with the support of the McKnight Foundation and the National Alliance for Research on Schizophrenia and Depression. We are currently continuing our studies of memory-related activity in cerebral cortex with the goal of establishing the origin and distribution of these signals. Our efforts is focused on two projects.

FUNCTIONAL SPECIALIZATION OF THE TEMPORAL AND PARIETAL PATHWAYS FOR MEMORIES. The results described above showed that there were differences in the contributions of the temporal and parietal pathways to short term memories related to performing a match to sample task. We are now performing a direct comparison of temporal and parietal cortex using two tasks that we believe are likely to differentiate the special contributions of these regions. We have trained animals to perform a task in which they must remember either the location *or* the shape of a sample stimulus. They must later make an either movement to the remembered shape or location when an array of test stimuli appear. We are recording from both temporal and parietal regions. It is our expectation that we will be able to prove that neurons in parietal cortex are preferentially involved when the animals must remember the location of the target, and that neurons in temporal cortex will be preferentially involved in remembering target shape. This project represents the first direct examination of region specialization for memory related neural signals.

NEURAL REPRESENTATIONS OF REMEMBERED TARGETS. Given the failure to demonstrate involvement of parietal cortex in representing remembered colors or motion in the match-to-sample task described above, we have been investigating classes of memory to which parietal cortex might contribute. We have recently discovered that a large proportion of parietal neurons are involved in representing the motion of objects that are temporarily lost from view.

Moving objects in the environment frequently disappear from view by passing behind an occluding objects. We nevertheless can accurately extrapolate the movements of such objects while they are not in sight. We have recorded the activity of neurons in the parietal cortex of monkeys while they preform a task that requires them to keep track of the location of targets, even when those targets disappear for a second or two. To our surprise, a large proportion (~40%) of neurons continued to fire action potentials when the stimulus disappeared, typically at a rate about half as great as when the stimulus was present. These same neurons were not active when the same stimulus disappeared on control trials in which the animal did not expect the stimulus to keep moving. We believe that these neurons provide the basis for an internal representation that keeps track of targets in the world, whether or not they are visible.

*Papers Published in Refereed Journals from work during Funding Period:*

Sclar, G., Maunsell, J.H.R., Lennie, P (1990) Coding of image contrast in central visual pathways of the macaque monkey. **Vision Res.** 30:1-10.

Merigan, W.H., Maunsell, J.H.R. (1990) Macaque vision after magnocellular lateral geniculate lesions. **Visual Neurosci.** 5:347-352.

Merigan, W.H., Katz, L. M., Maunsell, J.H.R. (1991) The effects of parvocellular lateral geniculate lesions on the acuity and contrast sensitivity of macaque monkeys. **J. Neurosci.** 11:994-1001.

Maunsell, J.H.R., Sclar, G., Nealey, T.A., DePriest, D.D. (1991) Extraretinal representation by neurons in area V4 in the visual cortex of the macaque monkey. **Visual Neurosci.** 7:561-573.

Maunsell, J.H.R. (1992) Functional visual streams. **Current Opinion Neurobiol.** 2:506-510.

Ferrera, V.P., Nealey, T.A., Maunsell, J.H.R. (1992) Mixed parvocellular and magnocellular geniculate signals in visual area V4. **Nature** 358:756-758.

Maunsell, J.H.R., Gibson, J.R. (1992) Visual response latencies in striate cortex of the macaque monkey. **J. Neurophysiol.** 68:1332-1344.

Merigan, W.H., Nealey, T.A., Maunsell, J.H.R. (1993) Visual effects of lesions of cortical area V2 in macaques. **J. Neurosci.** 13:3180-3191.

Merigan, W.H., Maunsell, J.H.R. (1993) How parallel are the primate visual pathways? **Ann. Rev. Neurosci.** 16:369-402.

Page, W.K., King, W.M., Merigan, W., Maunsell, J.H.R. (1994) Magnocellular or parvocellular lesions in the lateral geniculate nucleus of monkeys cause minor deficits of smooth pursuit eye movements. **Vision Res.** 34:223-239.

*Papers in Referred Journals from work during Funding Period; In press:*

Ferrera, V.P., Rudolph, K., Maunsell, J.H.R. (1994) Responses of neurons in the parietal and temporal visual pathways during a motion task. **J. Neurosci.** 14:*(in press).*

*Book Chapters Published from work during Funding Period:*

Maunsell, J.H.R., Nealey, T.A., Sclar, G., DePriest, D.D. (1989) Representation of extraretinal information in monkey visual cortex *(in)* D. Lam *(ed.)* **Proceedings of the Retinal Research Foundation Symposium** 2:223-235.

Maunsell, J.H.R., Hochstein, S. (1991) Effects of behavioral state on the stimulus selectivity of neurons in area V4 of the macaque monkey. *(in)* B. Blum *(ed.)* **Channels in the Visual Nervous System: Neurophysiology, Psychophysics and Models.** Freund Publishing, Tel Aviv. 447-470.

Maunsell, J.H.R. (1993) Neuronal correlates of object representation. *(in)* T. Poggio, D. Glaser. *(eds.)* **Exploring Brain Functions: Models in Neuroscience.** John Wiley and Sons, Ltd., 195-202.

Maunsell, J.H.R., Ferrera, V.P. (1993) Extraretinal representations in visual areas of macaque cerebral cortex. *(in)* T. Ono, L.R. Squire, M.E. Raichle, D.I. Perrett, M. Fukuda *(eds.)* **Brain Mechanisms of Perception and Memory: From Neuron to Behavior.** Oxford University Press, Oxford. pp. 104-118.

Maunsell, J.H.R., Ferrera, V.P. (1994) Attentional mechanisms in visual cortex. *(in)* L.R. Squire et al. *(eds.)* **The Cognitive Neurosciences,** MIT Press, Cambridge, MA. pp. 451-461.

Maunsell, J.H.R., Ferrera, V.P. (1994) Parallel processing in monkey extrastriate cortex. *(in)* T.B. Lawton *(ed.)* **Computation Vision Based on Neurobiology,** Proceedings of SPIE 2054, pp.240-242.

*Invited Presentations during the Funding Period:*

Optical Society of America Symposium on Functional Specialization in Visual Cortex, Orlando, October 1989.

Electrotechnical Laboratory, Agency of Industrial Science and Technology, Tsukuba Science City, Japan, January 1990.

Electrotechnical Laboratory, Agency of Industrial Science and Technology, Tsukuba Science City, Japan, January 1990.

RIKEN Institute, Laboratory for Neural Information Processing, Wako, Japan, January 1990.

Nihon University School of Medicine, Department of Physiology, Tokyo, Japan, January 1990.

National Institute for Physiological Sciences, Okazaki, Japan, January, 1990.

International School for Advanced Studies Workshop on Computational and Biological Models of Visual Processing, Trieste, Italy, February 1990.

Office of Naval Research Workshop on Computational Neuroscience, Woods Hole, August 1990.

State University of New York at Buffalo, Department of Biophysical Sciences, September 1990.

Integrative and Behavioral Neuroscience Group Symposium on Sensorimotor Integration, Society for Neuroscience Annual Meeting, St. Louis, October 1990.

Columbia University, Department of Biological Science, New York, April 1991.

Harvard Medical School, Program in Neuroscience Annual Retreat, New Seabury, MA, April 1991.

Johns Hopkins University, Department of Neuroscience, June 1991.

University of California San Francisco, Department of Physiology Spring Symposium, June 1991.

Baylor College of Medicine, Division of Neuroscience, July 1991.

International Brain Research Organization Symposium on Parallel Pathways in Vision, Montréal, August 1991.

International Symposium on Brain Mechanisms of Perception and Memory, Toyama, Japan, October 1991.

McKnight Foundation Conference on Neuroscience, Woods Hole, April 1992.

Association for Research in Vision and Ophthalmology Symposium on Parallel Visual Channels in Primate, Sarasota, Florida, May 1992.

FASEB Summer Research Conference on Biology, Chemistry and Modelling of Vision: Visual Processing, Saxtons River, VT, June 1992.

*Volunteered Presentations during the Funding Period:*

Maunsell, J.H.R. (1989) Motion processing in visual cortex.**Opt. Soc. Am. Tech.**

**Digest** 18:80.

Merigan, W.H., Byrne, C.E., Maunsell, J.H.R. (1989) Role of the magnocellular pathway in primate vision. **Soc. Neurosci. Abstr.** 15:1256.

Merigan, W.H., Byrne, C., Maunsell, J.H.R. (1990) Does motion perception depend on the magnocellular pathway? **Soc. Neurosci. Abstr.** 16:962.

Merigan, W.H., Pasternak, T., Polashenski, W., Maunsell, J.H.R., (1991) Permanent deficits in speed discrimination after MT/MST lesions in a macaque monkey. **Invest. Ophthalmol. Vis. Sci.** 32:824.

Pasternak, T., Maunsell, J.H.R., Polashenski, W., Merigan, W.H., (1991) Deficits in global motion perception after MT/MST lesions in a macaque. **Invest. Ophthalmol. Vis. Sci.** 32:824.

Page, W.K., King, W.M., Merigan, W.H., Maunsell, J.H.R., (1991) Motion detection deficits revealed by step ramp tracking errors in monkeys with magnocellular LGN lesions. **Invest. Ophthalmol. Vis. Sci.** 32:1021.

Ferrera, V.P., Maunsell, J.H.R. (1991) Responses of single units in macaque V1 to moving patterns. **Soc. Neurosci. Abstr.** 17:177.

Merigan, W.H., Pasternak, T., Ferrera, V., Maunsell, J.H.R. (1991) Permanent deficits in speed discrimination after MT/MST lesions in macaque monkeys. **Soc. Neurosci. Abstr.** 17:8.

Pasternak, T., Maunsell, J.H.R., Ferrera, V., Merigan, W.H. (1991) Global motion perception after MT/MST lesions in a macaque. **Soc. Neurosci. Abstr.** 17:8.

Page, W.K., King, W.M., Merigan, W.H., Maunsell, J.H.R. (1991) Eye movement deficits revealed by step ramp tracking errors in monkeys with magno and parvocellular LGN lesions. **Soc. Neurosci. Abstr.** 17:860.

Nealey, T.A., Maunsell, J.H.R., Merigan, W.H. (1992) Visual function after a lesion of cortical area V2 in the macaque. **Invest. Ophthalmol. Vis. Sci.** 33:1130.

*Training Activity during the Funding Period:*

GRADUATE STUDENTS:

†Tara A. Nealey, Ph.D. Physiology, April 1992, "Magnocellular and parvocellular contributions to cytochrome oxidase compartments in V1 of the macaque monkey".

Jay R. Gibson, Graduate Student in Neuroscience, 1990 to present, "Three-dimensional shape representation in area TE of the behaving monkey".

POSTDOCTORAL FELLOWS:

Vincent P. Ferrera, Ph.D. University of Chicago, 1989 to 1992, "Behavioral modulation of single unit activity in area MT".

John A. Assad, Ph.D. Harvard University, 1991 to present, "The role of posterior parietal cortex in target selection".

‡Sidney R. Lehky, Ph.D. University of Chicago, 1991 to 1994, "Neurophysiological basis of binocular rivalry".

†female, ‡minority

*Honors/Awards during the Funding Period:*

Dr. John Maunsell, McKnight Foundation Development Award
Dr. John Assad, National Research Service Award from National Institutes of Health.
Dr. Tara Nealey, National Research Service Award from National Institutes of Health.